A Comparison of Two Florida Populations of the Coquina Clam, *Donax variabilis* Say, 1822

(Bivalvia : Donacidae)

I. Intertidal Density, Distribution and Migration [1]

BY

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(8 Text figures)

INTRODUCTION

Donax variabilis Say, THE COQUINA CLAM, lives in the surf zone on sandy exposed beaches of the eastern United States and the northern Gulf of Mexico. The nomenclature of this species was, until recently, in a state of confusion. MORRISON (1970, 1971) pointed out that the correct name for the species is *Donax protracta* Conrad, 1849. However, the name *Donax variabilis* Say, 1822 was proposed for conservation (BOSS, 1970) and subsequently accepted by the I.C.Z.N. (MELVILLE, 1976).

Donax variabilis occupies the intertidal zone from the high (EDGREN, 1959) to low tide mark (PEARSE, *et al.*, 1942). Densities are variable, to a maximum of about 15600/m² (EDGREN, *op. cit.*). Many authors (ALDRICH, 1959; LOESCH, 1957; PEARSE, *et al.*, 1942; TIFFANY, 1971; TURNER & BELDING, 1957) have noted intertidal migrations of *D. variabilis*. TIFFANY (*op. cit.*) and TURNER & BELDING (*op. cit.*) have stated that this migratory behavior is stimulated by the acoustic shock of breaking waves. Contrarily, only once (EDGREN, *op. cit.*) has *D. variabilis* been reported as nonmigratory. I report here a second case of a nonmigratory population, even greater densities, and possible explanations for the intertidal distribution of two populations of *D. variabilis*.

MATERIALS AND METHODS

Coquinas were collected once each month, from April through September, 1976, from the intertidal zone of exposed sandy beaches on the central eastern (Indialantic Beach; 28°5.7′N Lat., 80°33.4′W Long.) and southwestern (Sanibel Island; 26°25.3′N Lat., 82°4.8′W Long.) coasts of Florida (Figure 1). The transect method of sampling was used (Figure 2.) An initial sample was collected at the point of maximum wave recession at the time of sampling. Additional samples were taken at 1 m intervals along transect A, normal to the beach face, to the point of maximum wave advancement at the time of sampling. The latter point was nearest the backshore and became saturated only temporarily by the swash of the waves. Transects B, C, and D were at 25 m intervals. Transects E, F, G, and H were 5 m apart. The closer-spaced transects were selected to eliminate the possibility of missing localized aggregations by using too large a sampling interval. The number of cores taken per monthly sample varied due to changing width of the swash zone, with a monthly average of 40 cores at Sanibel Island and 49 at Indialantic Beach.

At Indialantic Beach, collections were taken about 3 hours after low tide, on the rising lowest tide of the month, and precisely at low tide on the lowest ebb tide of the preceding weekend at Sanibel Island, except the first collection (April, 1976) which was made midway between a low and a high tide. This change in timing at Sanibel Island was made after having observed the nonmigratory behavior of the *Donax* on that beach.

Specimen samples were collected, using a 15.0 cm diameter (0.018 m²) polyvinyl chloride (PVC) corer, to a depth of 10 cm. Because the clams are restricted to the uppermost 4 cm of sand (EDGREN, 1959), the core contained all living specimens. Samples were sieved, using a 1.2 mm

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mesh. Sand samples were taken in an identical fashion, immediately adjacent to the specimen cores, but with a 5.0 cm diameter corer and to a depth of 4 cm. Standard granulometric sieve analyses (INMAN, 1952) were conducted on each sample.

Surf zone water temperature was measured to ± 0.5° C, and salinity was taken by refractometer to the nearest 0.5‰. Beach profiles were measured by triangulation (KING, 1972) at 1 m intervals from the seaward limit of dune vegetation to the base of the surf zone at the time of sampling. Wave height of 10 consecutive waves at their breaking point was measured using a graduated staff.

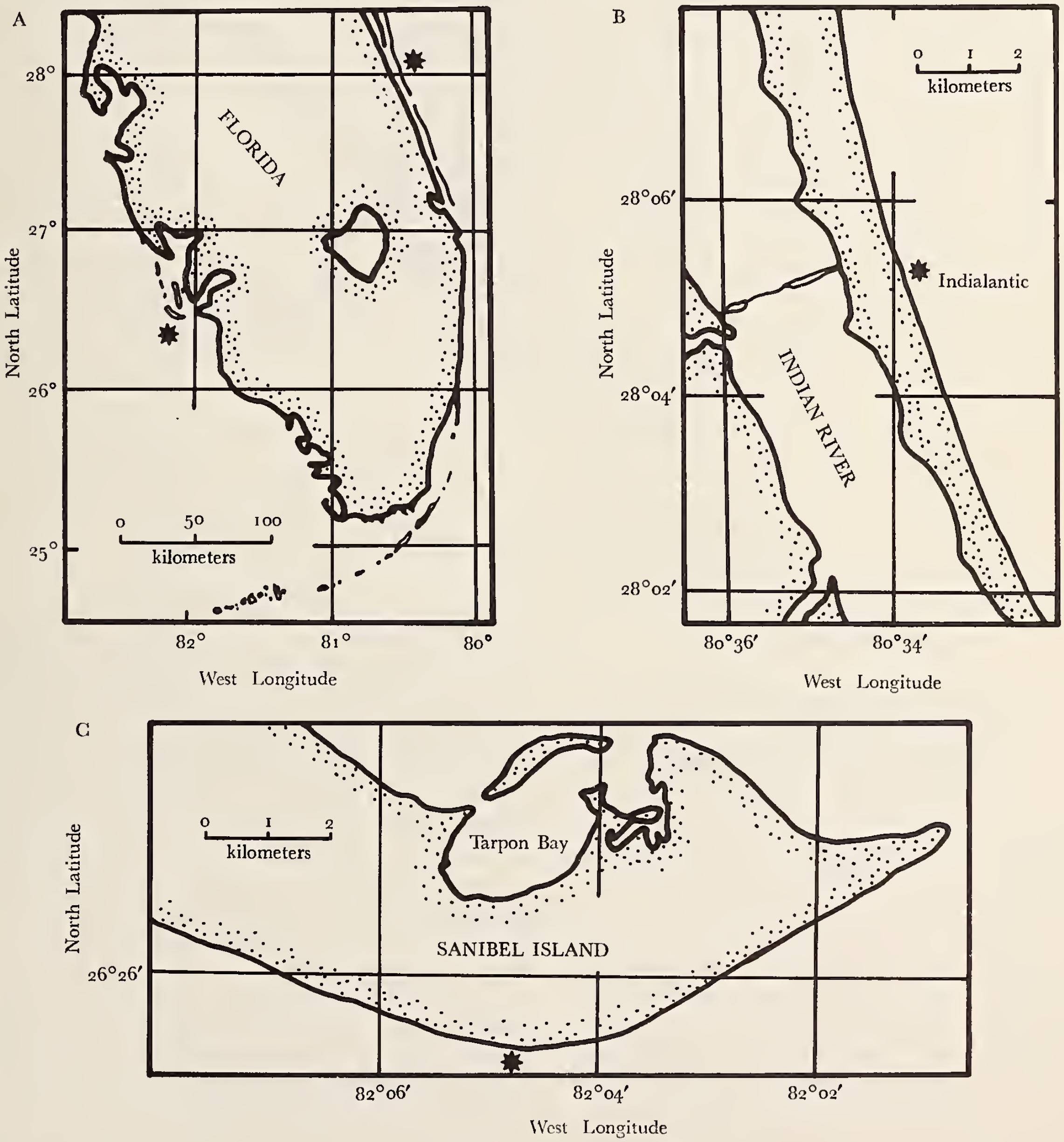

Figure 1

Location of sample sites (*): (A) General location; (B) Indialantic Beach and (C) Sanibel Island

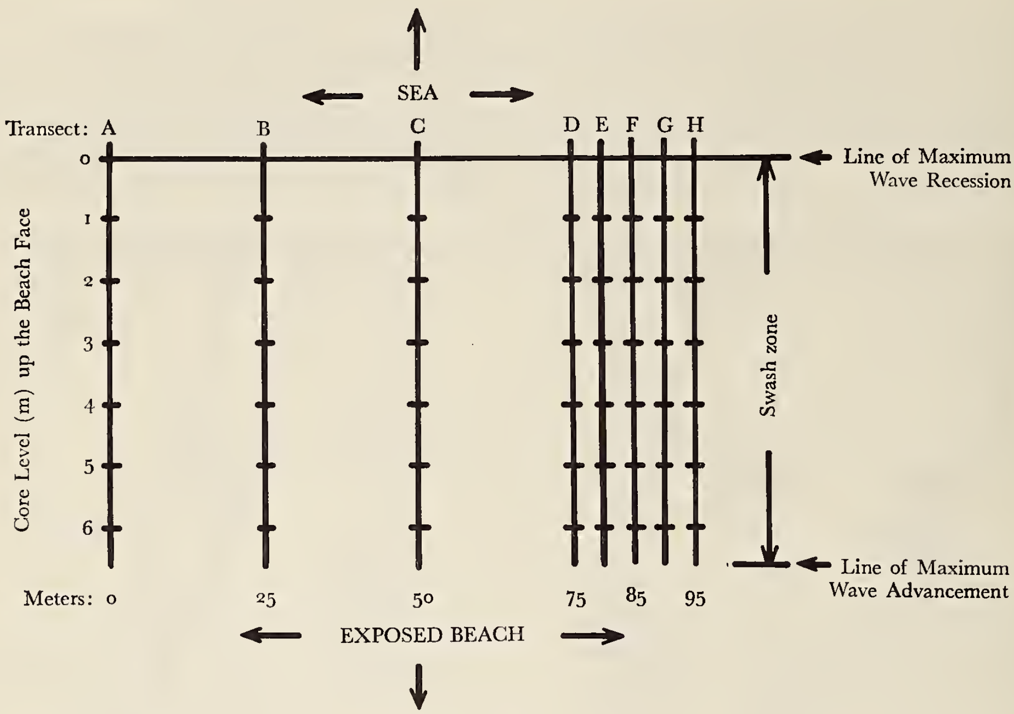

Figure 2

Diagrammatic representation of the sampling grid

RESULTS

Beach slope exhibited a mean drop of about 5.2 cm/m (a slope of 3.0°) at Sanibel Island and 12.0 cm/m (a slope of 6.9°) at Indialantic Beach. The beach at Sanibel appeared to be slightly more stable than Indialantic Beach, based on comparison of slope variation (Figure 3). Mean wave height was 23 cm at Sanibel and 91 cm (4 x greater) at Indialantic. Irregular semidiurnal tides at Sanibel ranged about 0.8 m, while at Indialantic Beach the tides were regular semidiurnal and averaged 1.2 m (Doty, 1957; U.S. Coast and Geodetic Survey, 1975), or 1.5 x greater than the range for Sanibel Island. Surf zone temperature and salinity ranges were 21.0-27.5°C and 30.0-35.0‰ at Sanibel Island, while at Indialantic Beach the ranges were 23.0-27.5°C and 30.0-36.0‰.

The mean particle size (D_{50}) of the sand was 0.58 mm (coarse sand; Wentworth, 1922) on Indialantic Beach and 0.26 mm (medium sand) on Sanibel Island. Mean particle size at Indialantic generally decreased progressing up the beach face, while at Sanibel the mean particle size remained relatively constant (Figure 4a). Both beaches had a uniform sand (uniformity coefficient $= D_{60}/D_{10} < 5$) with Sanibel Island being comparatively less uniform than Indialantic Beach (D_{60}/D_{10} = 3.14 and 2.61, respectively). The less uniform sand at Sanibel Island was due to the presence of an abundance of variably-sized large shell fragments. Mean particle size and uniformity coefficients were nearly constant between transects, although some variation in the uniformity coefficient was evident at Sanibel (Figures 4b, 5b). This slight variation was probably due to the sorting and subsequent deposition of large shell fragments by waves, and beach scalloping.

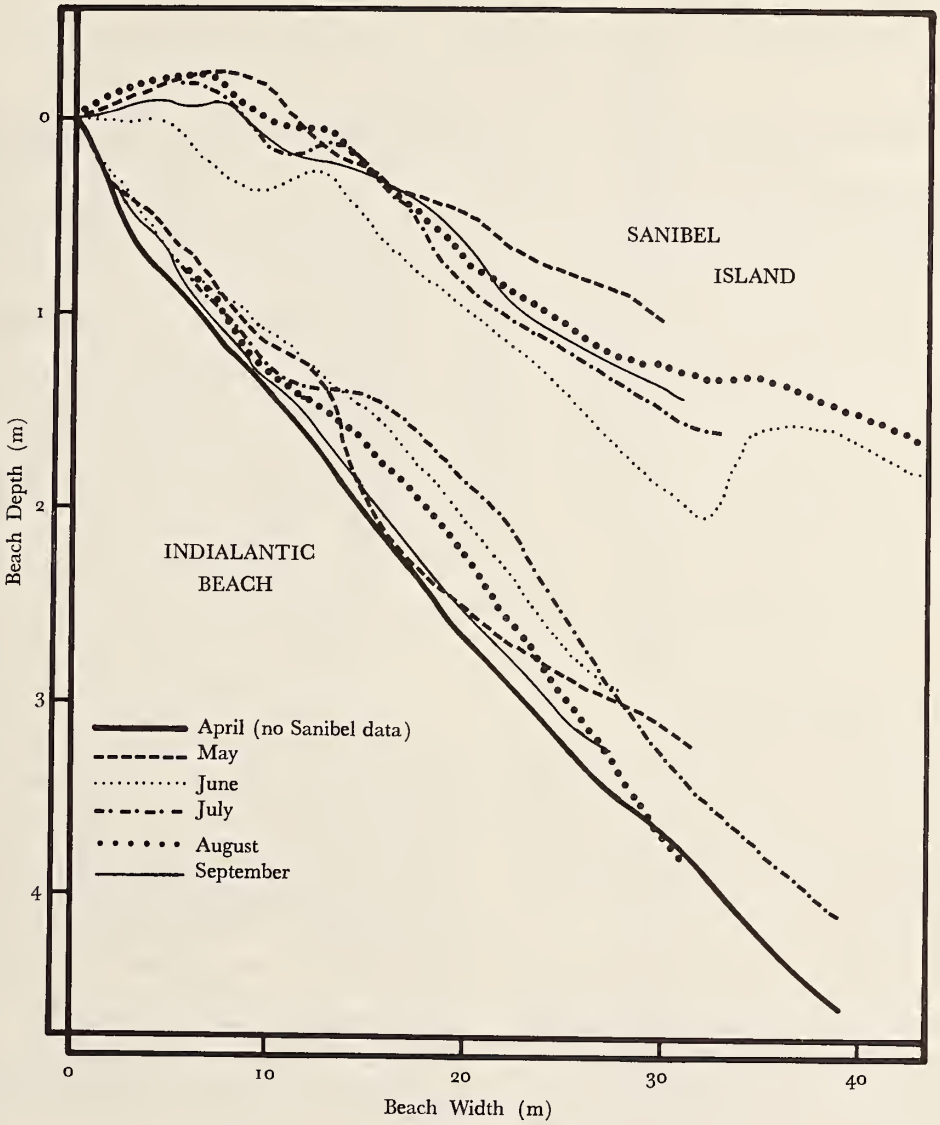

Figure 3

Beach profiles

A total of 28 832 specimens of *Donax variabilis* were collected from Sanibel Island, and 477 from Indialantic Beach. The ratio of Sanibel to Indialantic *Donax* per linear meter of beach was 60:1 (Table 1). At either location, there was little difference in numbers collected per transect between those at 25 m intervals and those 5 m apart. However, because the Sanibel Island clams were concentrated in the lower intertidal levels and the Indialantic Beach *Donax* were more dispersed in the wider surf zone, the ratio of the density per square meter of Sanibel to Indialantic *Donax* was, on the average, 80:1 (Table 1). These ratios are based on a monthly average of 33 372 individuals at Sanibel and 552 at Indialantic per linear meter of beach, and mean densities of 7 141/m² at Sanibel and 88/m² at Indialantic (Table 1). However, common densities at Sanibel frequently reached 20 000/m² and

Table 1

Density and numbers.

	N/m² of area sampled		N/linear m of beach		Sanibel Island				Indialantic Beach			
					Transects				Transects			
	Sanibel	Indialantic	Sanibel	Indialantic	A-D	E-H	Total	# cores	A-D	E-H	Total	# cores
April	72	39	342	200	42	7	49	38	12	17	29	41
May	10395	96	36383	672	3561	1678	5239	28	43	54	97	56
June	2654	166	16919	1058	1220	1216	2436	51	41	111	152	51
July	13114	124	62292	714	4179	4791	8970	38	37	66	103	46
August	5424	49	32544	343	1738	2948	4686	48	20	29	49	56
Sept.	11189	54	51749	324	4081	3371	7452	37	31	16	47	48
Total	—	—	—	—	14821	14011	28832	240	184	293	477	298
Mean	7141	88	33372	552	2470	2335	4805	40.0	31	49	80	49.7
Std. Dev.	5210	50	22563	321	1715	1708	3249	8.3	12	36	46	5.9
Coeff. of variation	73%	57%	68%	58%	69%	73%	68%	20.8%	39%	73%	58%	11.8%

once reached 60 000/m² in a small localized area during September. At Indialantic in June and July, densities were commonly 1 500/m², with a maximum of 2 500/m² for a localized area during July. Intertidal distribution and density was patchy at both beaches, but *Donax* seemed to "prefer" the shallower beach slope, finer sand, and lower wave energy of Sanibel Island.

The Indialantic population was always near the center of the swash zone (Figure 6). The clams were active, and made frequent migrations up and down the beach face, assisted by the wash of the surf. Although at each low tide the Indialantic *Donax* were washed into the subtidal region (personal observation), they regained their intertidal position with the subsequent incoming tide. At Sanibel, the *Donax* were nonmigratory and existed in high concentrations in the lower fifth of the intertidal zone, in a band about 4-5 m in width (Figure 6a) and could be found at this position at any stage of the tide. There was little variation in the distribution of *Donax* down the length of the beaches (Figure 6b).

DISCUSSION

Population Density

Because no difference was noted in the abundance of predators or in environmental parameters between sample sites (Mikkelsen, unpublished data), the large difference in the population of *Donax variabilis* may be attributed to the physical differences in the habitats, e.g., the beach profiles, wave energy, and sand grain size. The clams' "preference" for a shallower sloped beach can be supported in part by Edgren's (1959) observations on Clearwater Beach, Florida ". . . . that conditions near the pier, which resulted from or were reflected in the shallower slope of the beach, were somewhat more favorable for *Donax* than they were further north," where the beach "became progressively steeper." It was presumably the wave moderating action of a nearby pier which decreased the wave height on this section of beach, producing a shallow beach

Explanation of Figures 4 and 5 on the following page

Figure 4

Variation of mean sand particle size with (A) core level and (B) transect (——— Sanibel; – – – Indialantic)

Figure 5

Variation of uniformity coefficient with (A) core level and (B) transect (——— Sanibel; – – – Indialantic)

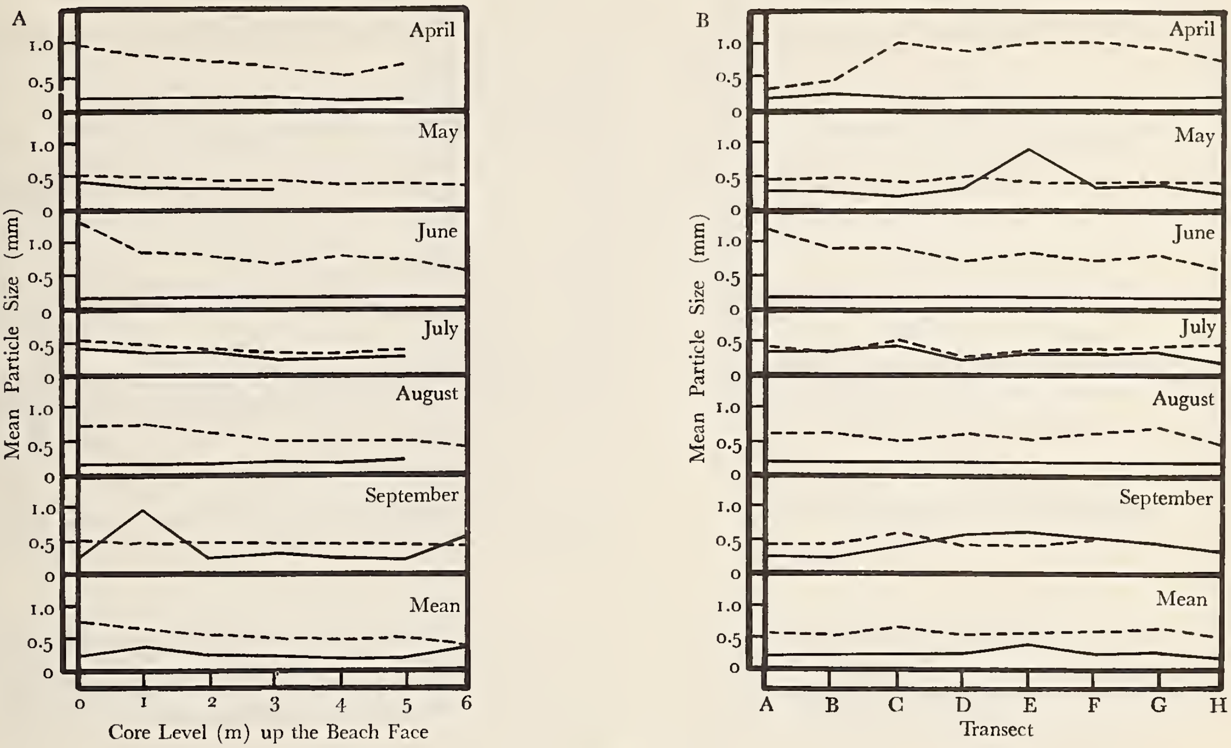

Figure 4

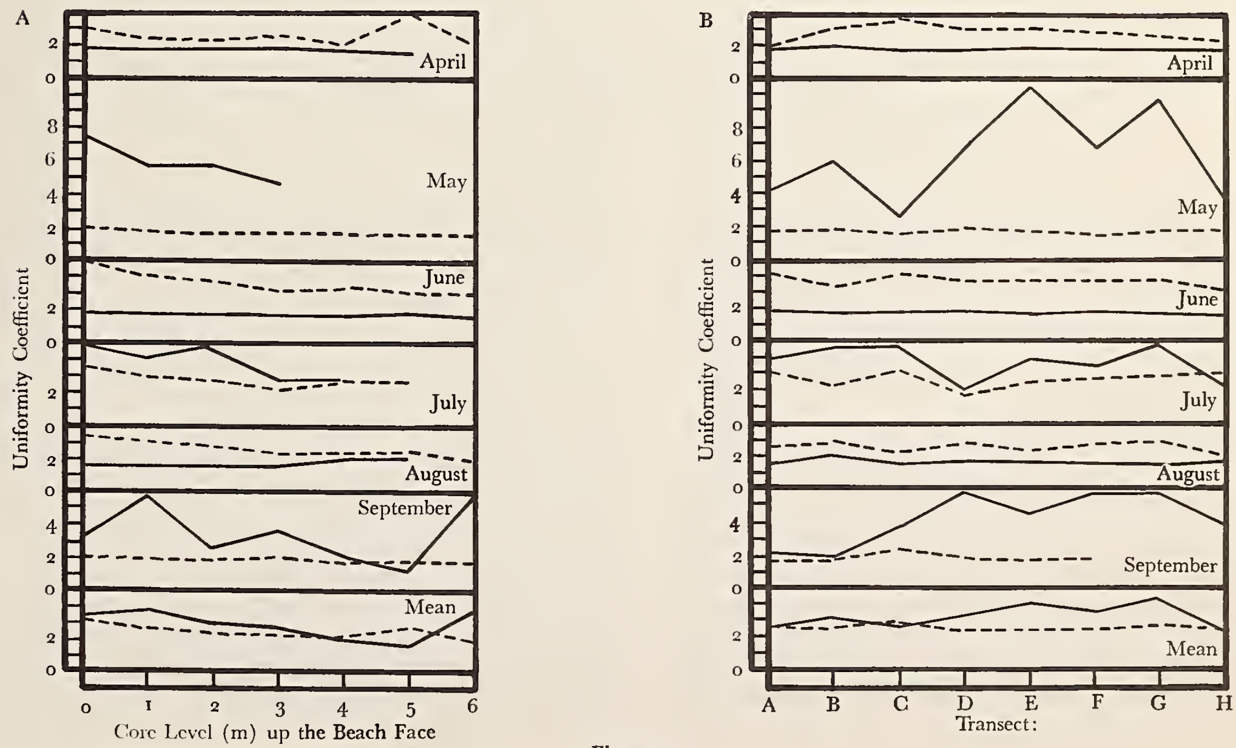

Figure 5

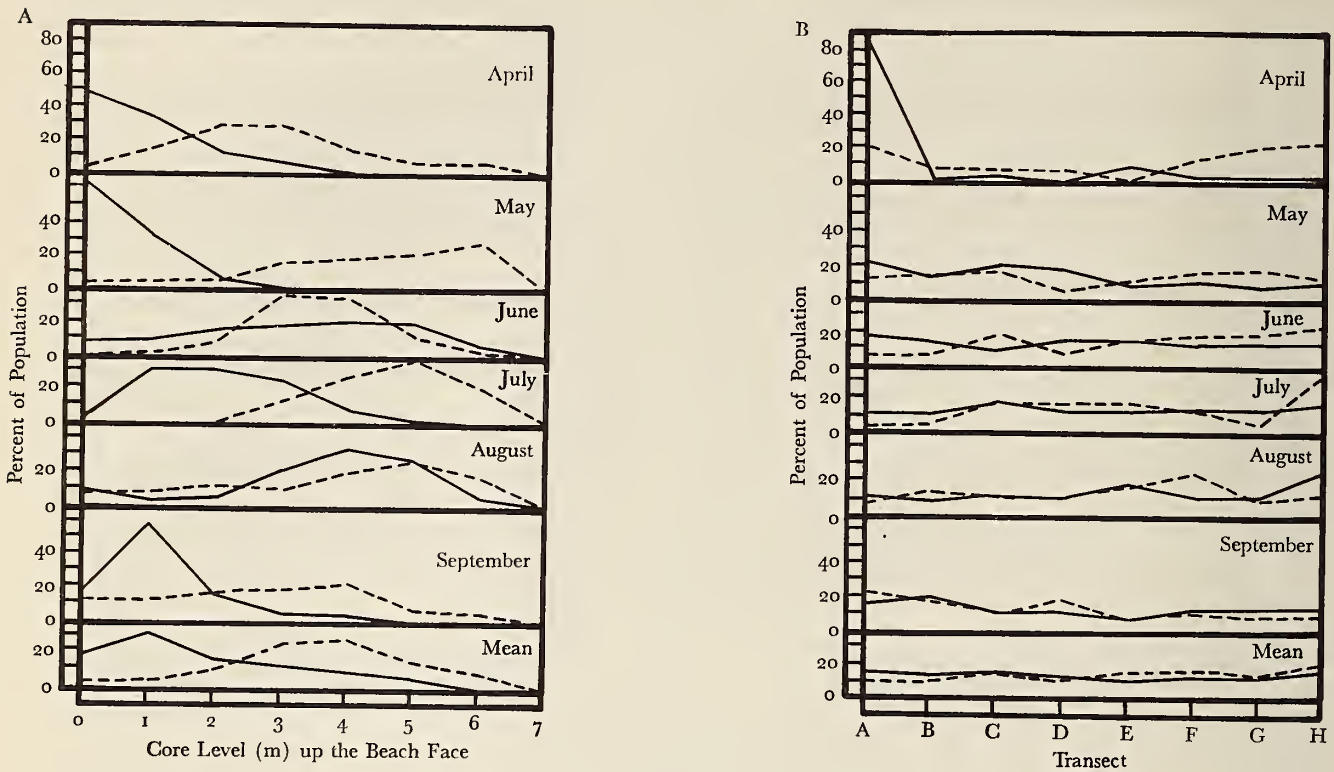

Figure 6

Location of the population of *Donax variabilis* as it varied with (A) core level and (B) transect (——— Sanibel; – – – Indialantic)

slope which Edgren described as "somewhat more favorable for *Donax*." The lower intertidal levels at Sanibel were often very crowded with individuals. These extremely high densities may be the result of the nonmigratory behavior in the presence of wave action, resulting in the subsequent deposition and accumulation of animals at the lower intertidal level.

The size of the *Donax* populations also appeared to fluctuate with the change in beach profile. For example, the decrease in the intertidal population at Sanibel in June (Table 1) may have been caused by the same conditions which removed a large amount of sand from the beach (Figure 7). As a consequence, a portion of the population may have been washed into the subtidal region, thus becoming unable to readily regain its intertidal position by the time of sampling. Similarly, at Sanibel in July, an increase in both population size and area under the beach profile occurred, indicating the deposition of both sand and *Donax* into the intertidal region, probably from subtidal areas. The small yield of specimens from the first collection in April at Sanibel was not because the specimens were washed offshore, but rather because the collection was taken midway between a low and high tide. Because of this sampling strategy, it appears that the population which had remained in the lower intertidal region and did not migrate up the beach face with the incoming tide was almost completely missed. Salinity changes (Figure 8) during the sampling months did not appear to have influenced fluctuations in the size of the populations.

The dense, larger population of *Donax variabilis* at Sanibel Island may be considered resurgent, that is, periodically but irregularly experiencing nearly complete exterminations, especially during warm months, followed by re-establishment of the population in subsequent years

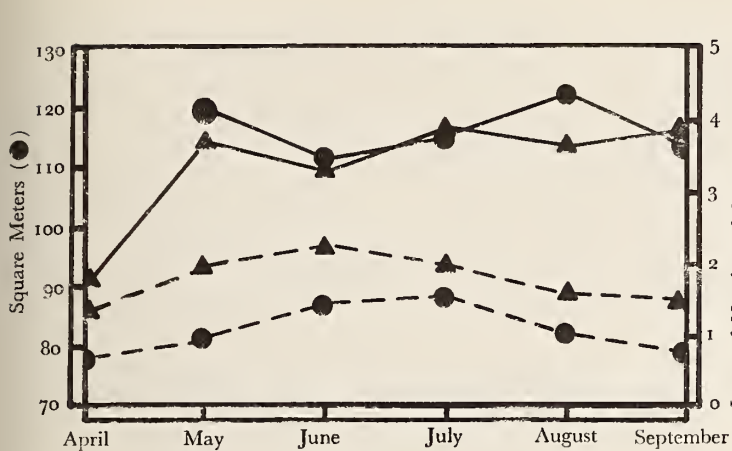

Figure 7

Number of *Donax variabilis* collected per month, and area under the beach profiles (——— Sanibel; - - - Indialantic)

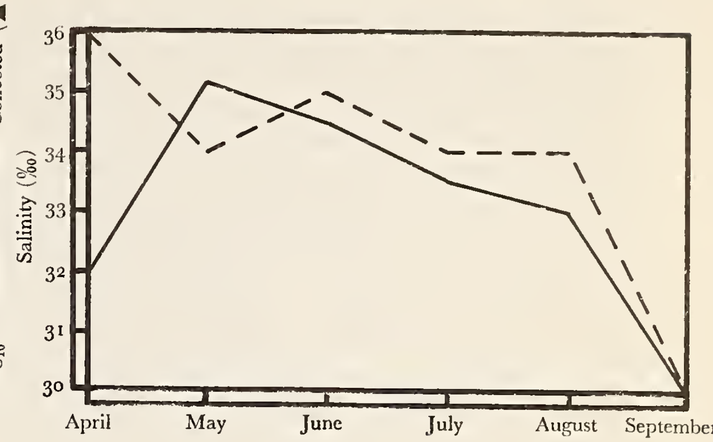

Figure 8

Monthly variation in surf zone salinity (——— Sanibel; - - - Indialantic)

(communication with Sanibel residents and personal observation). However, massive exterminations do not seem to occur at Indialantic Beach in populations of either *Donax variabilis* or the sympatric *D. parvula* Philippi, 1849. The cause of the Sanibel Island *Donax* population exterminations remains unknown. A possible explanation was provided by GUNTER (1947) who attributed massive oyster catastrophes in the Gulf of Mexico to high temperatures combined with excessive salinity. However, it is possible that he found only the indirect cause for such depletions. These temperature and salinity conditions could have facilitated an infestation of the clams by the parasite *Dermocystidium marinum* Mackin, Owen, and Collier, 1950, which is known to severely deplete populations of the oyster, *Crassostrea virginica* (Gmelin, 1791), in the Gulf of Mexico (MACKIN, 1951) and the Chesapeake Bay (see JOYCE, 1972). Although this aspect was not investigated, *Dermocystidium marinum* or other parasites may infest *Donax* and affect the population size.

COE (1957) stated that resurgent populations of *Donax* have been noticed on both coasts of the United States, but did not mention the species involved. Such resurgences have been noticed for *Donax gouldii* Dall, 1921 (COE, 1953, 1955, 1956; JOHNSON, 1966b, 1968), *Donax vittatus* DaCosta, 1778 (PELSENEER, 1928), and *Donax "tumida"* Philippi, 1849 (= *Donax texasiana* Philippi, 1847) (LOESCH, 1957). Extensive, rapid depletions in the size of *D. gouldii* populations have been attributed to such causes as exposure to freshwater emanating from a hot spring area and high temperatures (JOHNSON, 1966b), infestation by parasites (PELSENEER, 1928; COE, 1956), and various environmental and biological factors (JOHNSON, 1968). Thus, both biological and environmental factors may contribute to rapid population declines in the genus *Donax* and probably for *D. variabilis*.

Migratory Behavior and Intertidal Distribution

Many authors (ALDRICH, 1959; ANSELL & TREVALLION, 1969; EDGREN, 1959; JACOBSON, 1955; JOHNSON, 1966a, 1966b; MORI, 1938, 1950; POHLO, 1967; STOLL, 1937, 1938; TIFFANY, 1971; TRUEMAN, 1971; TURNER & BELDING, 1957; WADE, 1964, 1965, 1967a, 1967b; IRWIN, 1973) have reported on the intertidal migrations of *Donax* spp. and speculated on or tested the stimulus for migration. In addition to *D. variabilis*, other species of *Donax* noted to be nonmigratory are *D. gouldii* (see HEDGPETH, 1957; POHLO, *op. cit.*), *D. faba* Gmelin, 1791, and *D. vittatus* DaCosta, 1778 (see ANSELL & TREVALLION, *op. cit.*). In considering the many reports involving intertidal migrations, it is unfortunate that only a few (EDGREN, *op. cit.*; JOHNSON, 1966a; TURNER & BELDING, *op. cit.*; WADE, 1967a) have noted such parameters as beach slope, wave impact, and sand particle size in an attempt to correlate these factors with migrations. TIFFANY (*op. cit.*) and TURNER & BELDING (*op. cit.*) experimentally determined that the migratory behavior of *D. variabilis* was controlled by the acoustic shock/stimulation of the breaking waves on the beach.

EDGREN'S (1959) observations on Clearwater Beach and my own on Sanibel Island (both on the west coast of Florida) showed *Donax variabilis* to be nonmigratory. However, Edgren observed that the *Donax* maintained a position near the high tide mark while my observations showed the species to maintain a very low intertidal position. Although the wave size at Sanibel (a low energy beach) may be small, the population surely experienced some degree of acoustic wave shock, and yet the clams were not stimulated to migrate. Nonmigratory behavior of both the Clearwater Beach and Sanibel Island *Donax* populations may also be influenced by beach slope. However, it is difficult to compare Sanibel's slope of 3.0° with Edgren's non-quantitative "quite gentle slope." On Turner Beach, Captiva Island, about 15 km northwest of the Sanibel sample site, where the beach slope, wave impact, and sand grain size are greater, *Donax variabilis* is migratory. The nonmigratory behavior of the Sanibel Island *Donax* could thus be a result of, or the lack of one or a combination of these factors. The combination of small waves and low beach slope causes large areas of the beach to be exposed with a small drop in the tide, thereby inhibiting the ability of *Donax* to follow the tide. If regular migrations did occur at Sanibel, the individuals could easily become stranded above the swash zone for long periods of time due to the irregular semidiurnal tide. By maintaining a low intertidal position, the Sanibel *Donax* avoided this.

In addition to beach profiles, tidal regime, and wave energy, sand particle size and permeability may affect *Donax* intertidal migrations and distribution. At Indialantic, *Donax* had no apparent difficulty in burying in the coarse sand. At Sanibel, many clams did not, or probably could not bury themselves completely, and once dislodged were washed about on the surface of the sands throughout several consecutive wave periods before partially resecuring themselves in the sand. The Sanibel sand is of medium grain size and is firm when wet. This sand has a permeability (see KRUMBEIN & MONK, 1942) an order of magnitude lower than Indialantic Beach sand, and is not appreciably loosened by wave wash. The movement of the clams by waves had a tendency to concentrate and deposit the individuals in the lower intertidal zone (Figure 6a). This concentration and deposition was similar to that of the larger sand and shell fragments (Figures 4a, 5a).

SUMMARY

Donax variabilis Say, 1822 was collected monthly from late spring to early fall of 1976 from two locations on the central eastern (Indialantic) and southwestern (Sanibel Island) coasts of peninsular Florida. Sanibel Island supported a population of *D. variabilis* 60 times greater in size and 80 times as dense as that of Indialantic Beach, probably due to lower beach slope and wave energy at Sanibel. Intertidal migrations occurred constantly at Indialantic Beach, with the *Donax* maintaining a position about the center of the swash zone. Sanibel Island *Donax* were nonmigratory and lived predominantly at low intertidal levels. This unusual nonmigratory behavior is thought to be a local adaptation to cope with the combination of low beach slope and wave energy in conjunction with irregular semidiurnal tides and low sand permeability. Therefore, the magnitude and degree of beach slope, tidal regime, wave energy, and sand particle size and permeability necessary for intertidal migrations of *D. variabilis* remain uncertain.

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